

Effect of increased food abundance near forest edges on flocking patterns of Coal Tit *Parus ater* winter groups in mountain coniferous forests

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Capsule Individuals concentrated near forest edges in bigger social groups than in forest interiors and foraged more on pine cones which were more abundant there.

Aims To evaluate differences in food distribution between forest edges and forest interiors and their effects on the non-breeding flocking patterns of Coal Tit populations inhabiting mountain coniferous forests.

Methods We collected cone production data at forests edges and interiors in mountain pine forests located in the Pyrenees (northeast Iberian peninsula). At the same sites, we also quantified Coal Tit abundance, flocking patterns and foraging behaviour by means of paired bird surveys during autumn and early winter.

Results We recorded a larger abundance of pine cones available on trees along forest edges compared with forest interiors. Coal Tit groups were of bigger size along forest edges, although the number of social groups detected did not differ from forest interiors. Our observations on foraging behaviour supported the hypothesis that differences in flock sizes and overall abundances associated with distance to the edge are due to differences in the availability of pine cones and to the heavier use of these foraging substrates by birds along forest edges.

Conclusions Our results suggest that by changing food distribution, edge effects on pine cone production may be significantly involved in local changes in the social structure of the Coal Tit. An increase in resource heterogeneity and local population density may have important implications at a population level, such as favouring mobility of individuals searching for food resources and thus a transient life, and increasing the costs of territory defence to resident individuals.

Habitat boundaries have traditionally been subjected to examination because of their special role in determining community structure (Yahner 1988). Sharp boundaries, such as forest edges, introduce heterogeneity to forest habitats. They often have very different ecological characteristics than forest interior habitats, mainly resulting from different abiotic conditions near edges (Chen *et al.* 1992, Murcia 1995). Increased sunlight incidence and reduced competition may enhance vegetative growth at particular forest edge sites (Chen *et al.* 1992). As a consequence, edge vegetation often differs from that found at the forest interior (Boutin & Jobin 1998). Changes in vegetation characteristics and local abiotic factors, such as wind incidence near forest edges, are usually associated with

changes in species distribution affecting fundamental ecological processes such as patterns of animal movement (Desrochers & Fortin 2000), nest predation and brood parasitism (Paton 1994) or foraging ecology (Huhta *et al.* 1999, Dolby & Grubb 1999). Many specific animal responses to edges have been described (Hanson 1983, Yahner 1988, Hawrot & Niemi 1996). However, our understanding of mechanisms leading to observed avoidance or selection of areas near edges (edge effect) and their implications for bird behaviour and social patterns is usually limited to speculation (Lima & Zollner 1996).

During the non-breeding season, Parids form groups of variable size and degree of residence (Matthysen 1990). Food distribution within territories seems an important factor behind their social structure, influencing home range size, territoriality and flock stability (Smith & Van Buskirk 1988, With & Morrison 1990). Alternatively, predation pressure is also important in

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determining habitat selection and flocking patterns (Rodríguez *et al.* 2001). We examine differences in food distribution between forest edges and interiors and their effects on the flocking patterns of Coal Tit populations inhabiting mountain coniferous forests. We specifically tested whether Coal Tits respond to forest edges because (1) vegetation changes near edges (vegetation hypothesis) or because (2) changes occur in foraging site and foraging success near boundaries (food hypothesis). We first examined whether increased light exposure and reduced competitive stress in mountain pines located near forest edges result in a larger cone production when compared to that of pines in forest interiors. Second, we focused on how vegetation changes associated with cone production affected Coal Tit flocking patterns. We predicted that differences in food distribution affects Coal Tit flocking patterns by concentrating individuals and increasing flock sizes on locations where pine cone production is greater.

METHODS

The study area was located in the Pyrenees mountain range, at 1800–2000 m asl (northeast Iberian peninsula). Subalpine coniferous forests here are dominated by the Mountain Pine (*Pinus uncinata*) and secondarily

by the Scots Pine (*Pinus sylvestris*). Edges were defined as abrupt changes in habitat type, typically between coniferous forests and pastures or open areas. These are created in two ways in these mountain areas. Natural disturbances such as avalanches disrupt forest continuity by increasing the amount of edges present. Furthermore, by creating open areas for livestock grazing or ski activities, human perturbation also results in an increase of forest edge length in these areas.

Bird surveys

Coal Tit foraging behaviour and flocking patterns were monitored from November to January after the opening of pine cones in October. We conducted bird surveys along edges (edge surveys) and in interior forest habitats (> 50 m from forest edges, interior surveys). We counted birds seen or heard within a 25 m belt on each side of the observer. We paired each forest edge survey with a forest interior survey (Fig. 1). The edge survey was conducted parallel to a forest edge and 25 m from it inside the forest. To homogenize location of surveys within each pair, the interior forest survey started 50 m from an edge, at the mid-point of its paired edge counterpart, and ran perpendicular to it. The surveys were conducted by walking a fixed distance of 250 m at a constant speed.

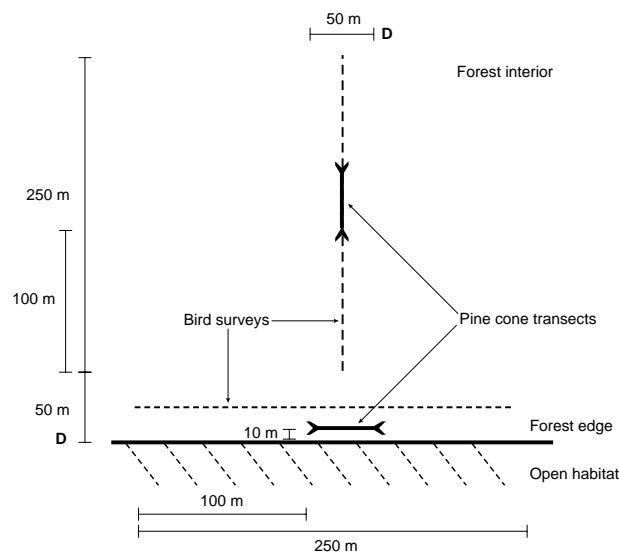


Figure 1. Schematic view of the field sampling procedure. At each forest site, we conducted two bird surveys (250 m long): interior survey (> 50 m from the edge) and edge survey (25 m from the edge). Detection belts (D) used in bird surveys were 25 m to both sides of the observer. Paired with each bird survey (in 8 bird survey pairs), we conducted an interior pine cone transect (50 m long, starting about 150 m from the edge) and an edge pine cone transect (50 m long, located 10 m from the edge).

Timing of surveys

We allowed a minimum of two hours between two consecutive surveys belonging to the same pair to allow birds to move around in the area and thus, avoid serial dependence in bird location. The order of walking edge and interior surveys was reversed in consecutive pairs. Since we did not colour-mark the birds in the present study, and to minimize the probability of detecting the same individuals in different survey pairs, we selected pairs of sites separated from each other by at least 1 km. Each pair of surveys was conducted the same day and in the same area, so that we were able to compare only the differences arising from survey location in relation to edge distance and not from temporally related differences in bird distribution. We conducted a maximum of two paired surveys per day with at least one week between consecutive fieldwork days. Enough time between fieldwork days also allowed for a turnover of transient individuals. While there was a small risk of observing juvenile residents in different sites, we considered this probability to be very low due to the low exchange rate among areas (Brotons 2000a).

Field recording

Each time Coal Tits were encountered along the surveys, we noted the number of individuals in a social group (i.e. individuals within auditory range as judged by the maximum distance to which an individual was heard by the observer while following the group). Given the easy auditory detectability of this species, we considered that vegetation change between edges and forest interiors did not affect probability of bird contact. This is unlikely to be the case for visual contacts, which are probably affected by changes in vegetation structure. Since nearly all the groups encountered during the surveys were first contacted by contact calls, we assumed that group detection rate and individual counts were the same in forest edges and in forest interiors and that this probability approached 1.

After the initial contact with a social group, we started recording the foraging behaviour of birds. We then focussed on the closest individual to the observer, and after 5 s we described its foraging location among the tree canopy by using five different categories: trunk, thick branches (> 1 cm diameter), twigs (< 1 cm), needles and pine cones. We then followed the movements of the focal individual and noted its foraging locations at 15 s intervals until out of sight. We then immediately changed the observations to its closest neighbour (see also Brotons 1997 for further details of foraging data collection). Only one observation per individual per tree was included in the analysis. At edge surveys, foraging observations located more than 40 m from the edge were discarded.

After a maximum of 10 min of recording foraging, or 50 m from the initial contact point with the focal group, the survey was resumed at the location where the flock had been encountered until another social group was located. We noted the direction of each recorded group to avoid encountering the same group twice during the same survey. In total, we conducted 13 pairs of surveys. We used non-parametric matched comparisons (Wilcoxon paired test, Sokal & Rohlf 1995) to compare total abundance, mean group size and number of groups per transect between forest edge and forest interior surveys. Differences in the use of substrates in forest interior and edges were assessed by chi-squared statistics (i.e. differences in frequency estimates between groups, Sokal & Rohlf 1995).

Measuring pine cone distribution and abundance

Pine cone production was studied in eight of the same

areas where the Coal Tit surveys were conducted. We used 50 m long-line transects (pine cone transects) at forest interiors and edges to estimate the availability of cones in each habitat type. We located the initial point of each pine cone transect 100 m from the starting point of a corresponding bird survey (Fig. 1). Edge transects ran parallel to a forest edge bird survey but were located only 10 m from the forest edge to give a better estimate of the cone production of pines adjacent to the edges. Interior transects exactly coincided with the trajectory of the corresponding bird survey.

In these pine cone transects, we ranked from 1 to 5 (according to the amount of pine cones as estimated from the percentage of branches containing pine cones) each pine tree encountered 5 m at each side of the transect. We assumed that all pine cones are similar in terms of seed availability (Genard & Lescourret 1986). Pines with cone classes 0 and 1 (class 0: pines with no cones present; class 1: pines with less than 5% of branches with at least one pine cone) were considered pines with low cone indexes, whereas, pines belonging to classes 4 and 5 (class 4: pines with more than 50% of branches containing cones; class 5: pines with more than 75% of branches containing pine cones, typically few cones per branch) were considered trees with high cone indexes. We also noted tree height and the distance to its nearest neighbour to obtain an estimate of tree density. Means for each variable were calculated per transect.

From parallel fieldwork in the study area, we were able to include five supplementary forest interior cone transects, which were not paired with bird surveys, and were located at least 100 m from their nearest neighbour. To obtain more accurate estimates of pine cone distribution at forest interiors, we analysed these pine cone transects together with the ones obtained at bird survey sites. The analyses included a total of 21 transects (8 located near a forest edge, 13 in forest interiors) with a total of 431 trees (mean = 20.5 trees per transect). We analysed possible differences in pine cone abundance between edge and forest interiors using ANOVA and ANCOVA using number of trees per transect, tree height and nearest neighbour tree as covariables. The proportion of trees per transect with low (low resource availability) or high pine cone indexes (concentration of food resources) were considered the most relevant descriptors of the spatial distribution of pine cone abundance in relation to its possible use by Coal Tits. These two variables required arcsin transformation to meet the requirements of parametric analyses (Sokal & Rohlf 1995).

RESULTS

Coal Tit numbers

Overall, we detected a higher number of Coal Tits along forest edge surveys than in forest interiors (Wilcoxon paired test, $Z = 2.69$, $n = 13$, $P < 0.01$, Fig. 2). However, the number of groups detected per survey did not differ between forest edges and forest interiors ($Z = 1.9$, $n = 13$, $P = 0.07$, Fig. 2). Therefore, the higher number of birds detected along forest edges was due to the larger flock sizes of groups foraging there, rather than to the presence of a larger number of social groups. Indeed, flock size of groups foraging along forest edges was significantly larger than that of those located in forest interiors ($Z = 2.73$, $n = 13$, $P = 0.01$, Fig. 2).

Coal Tits foraging in mountain pines located along forest edges used pine cones as a foraging substrate to a larger degree than did Coal Tits in forest interiors ($\chi^2_4 = 12.76$, $P = 0.012$, $n = 135$, Fig. 3). Individuals tended to use twigs and thick branches more in forest interior locations than at edges, whereas the use of trunks and needles remained similar in the two forest locations (Fig. 3).

Pine cone distribution and abundance

Mean cone index was negatively associated with pine height ($F_{1,16} = 45.54$, $P < 0.001$) but not to the distance between adjacent trees ($F_{1,16} = 0.11$, $P = 0.34$). Pine trees had a larger cone abundance along edges than in forest interior areas (mean cone index, forest edges = 2.25; forest interiors = 1.01; $F_{1,16} = 11.85$, $P < 0.01$).

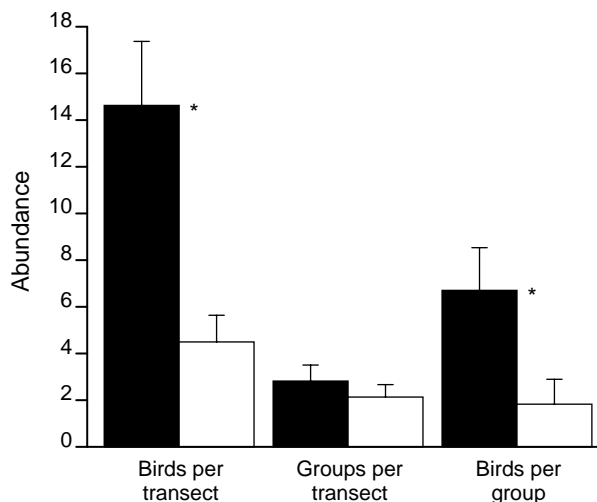


Figure 2. Coal Tit abundance patterns as measured from the surveys according to forest location ($n = 13$ pairs). Bars represent standard error. Asterisks show significant differences between forest edges and forest interiors tested with a Wilcoxon paired test.

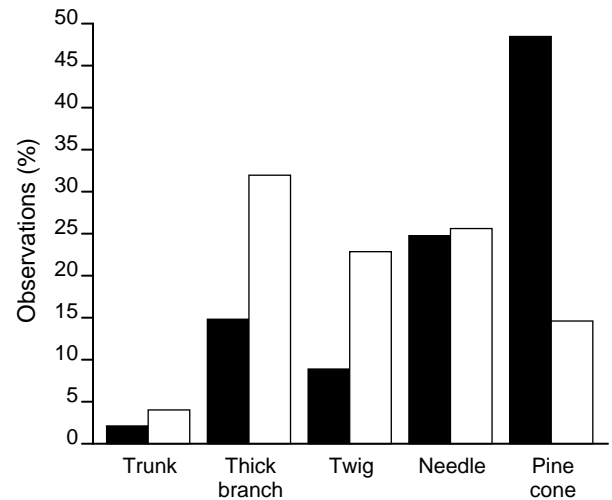


Figure 3. Foraging substrates used by Coal Tits along edges and forest interiors as observed during transect followings ($n = 135$ observations).

The proportion of pines without or very few cones (classes 0 and 1) was lower at forest edges (mean proportion at forest edges = 7.8 %; forest interiors = 33.8 %; $F_{1,19} = 13.01$, $P < 0.001$). However, the opposite was true for the proportion of trees with large pine cone indexes (classes 4 and 5), which were more abundant along forest edges (mean proportion at forest edges = 39.4 %; forest interiors = 15.4 %; $F_{1,19} = 6.45$, $P < 0.05$). After controlling for the effects of tree height and nearest neighbour tree distance, the mean proportion of trees with low cone indexes remained significantly higher in forest interiors ($F_{1,16} = 4.40$, $P < 0.05$). However, after controlling for the same variables, the proportion of trees with large cone indexes did not differ between edges and forest interiors ($F_{1,16} = 1.59$, $P = 0.22$).

DISCUSSION

Food source distribution in relation to forest edge location in subalpine coniferous forests was significantly associated with Coal Tit numbers and flocking patterns. During the non-breeding season, individuals of this species concentrated in flocks near edges, where mean cone production was higher.

Tree height and location within the forest were correlated with mean pine cone index, but not distance between neighbouring trees. Therefore, differences in the proportion of trees with large cone production between forest edges and interiors seemed mostly related to differences in tree size, whereas differences in the amount of low productive trees present might be

related to other environmental factors differing between forest edges and forest interior areas. These results suggest that tree age and abiotic factors related to location such as incidence of solar radiation are associated with cone production in our study area, whereas competition between trees does not strongly affect this parameter (see Genard and Lescourret 1986, 1987 for similar results). We argue that the larger cone production along edges might be associated with the higher and more homogenous productivity of younger trees (i.e. small trees, Freléchoux *et al.* 2000) located near edges, compared with the lower and more irregular cone crop distribution in forest interiors. This resulted in a highly heterogeneous spatial distribution of pine cones among trees in the studied forests.

Since resident birds usually travel alone or in pairs (Brotons 2000a), the larger group size of birds foraging along forest edges suggests that transients are likely to form the bulk of the flocks detected along edges. Coal Tit transient juveniles might be attracted by a locally rich but heterogeneous food resource, such as the pine cone crop of mountain pine forests. Flocking may enhance the location of a spatially heterogeneous food resource (Caraco & Pulliam 1980) and, therefore, may improve foraging prospects of juvenile birds in mountain coniferous forests in which cone crop is irregularly distributed in space. Alternatively, if predation risk is high near forest edges (Rodríguez *et al.* 2001), large group sizes there may also enhance predator detection and benefit individuals occupying risky microhabitats.

The number of social groups detected did not differ between interior and edge trials. The smaller group size in the interior of the forests, of about two individuals, may correspond to the spacing distribution of resident adult Coal Tits. These individuals have very restricted home ranges during the breeding season and only occasionally associate with transient juvenile birds in large flocks (Brotons 2000a). Since the Coal Tit is a hoarding species, resident individuals tend to have a more predictable food supply (Brotons 2000b, Broggi & Brotons 2001) and, contrary to transients, adopt a different foraging strategy with little need to exploit the relatively high pine seed resources at forest edges. In this context, by avoiding edges, residents could also benefit from a hypothetical increase in predation risk near forest boundaries (Rodríguez *et al.* 2001).

Our results suggest that edge effects on pine cone production may significantly be involved in changes in the social structure of some species by changing food distribution in rather homogeneous habitats such as conifer forests (Berner & Grubb 1985, Angelstram

1992). An increase in resource heterogeneity and local population density may have important implications such as promoting mobility and thus, favouring transient life and increasing the costs of territory defence to resident individuals (Smith & van Buskirk 1988, Brotons 2000a).

A recent study of behavioural responses of chickadees to forest boundaries, found that birds may use forest edges as movement conduits, resulting in these areas being used more often than expected by chance alone (Desrochers & Fortin 2000). These authors did not find any significant role of vegetation or foraging behaviour in the response of birds to forest edges, and interpreted edges as movement conduits that drive flock movement. We cannot discard the movement conduit hypothesis being behind the large number of individuals recorded along forest edges. However, the differences recorded in pine cone production and the differences in the foraging behaviour of Coal Tits strongly suggest that birds foraging near forest edges, probably mostly juvenile transients, were profiting from pine seeds which were not as widely available in the interior of the forest.

Since forest fragmentation increases the relative amount of edges in a landscape (Murcia 1995), this process might indirectly alter flocking patterns and sociality in forest passerines such as the Coal Tit, which may profit from enhanced levels of seed food source and, thus, increase mean flock size along forest edges. Flock size and composition in fragmented forests in a suburban area in Spain showed significant effects associated with the spatial arrangement of forest patches (Fernandez-Juricic 2000). However, this author found that fragment size and local habitat variables positively affected flock size in a guild of forest passerines. Further studies are needed to investigate how amount of edge habitat interacts with patch size and isolation in determining the social structure and flocking patterns of forest passerines. In mountain areas, recent development of ski resorts is increasing the amount of permanent edge areas without strongly increasing fragmentation of forest areas, which offers an appropriate framework to separate these effects.

In summary, forest boundaries are likely to induce an increase in the heterogeneity of forest habitats, particularly by inducing changes in vegetation characteristics or productivity. We have shown that forest edges in mountain pine forests contain trees with higher cone productivity than areas in forest interiors and this difference seems to have significant effects on the flocking pattern and foraging activity of birds.

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